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# Visual Target Detection in Damselflies

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# 1 Abstract

Insect predators accomplish difficult visual tasks with tiny visual systems, and may provide important information for machine vision and remote sensing applications in variable light environments. We studied the visual system of the damselfly *Megalagrion xanthomelas*, which possesses 1.5mm diameter eyes with 360° field of view, lives in dark habitats, and detects small objects against complex backgrounds. We accomplished four objectives: 1) Mapped regional variation in light sensitivity and spatial resolving power across the thousands of individual sensory units. Compound eyes (multiple, non-focusing lenses) may inspire microsensor array design. 2) Developed methods to quantify light heterogeneity viewed by the sensor array in nature along four principle viewing directions. These spectroradiometric measurements provide critical data on limits to target detection imposed by ambient brightness and color contrast. 3) Established color as an essential sensory channel for target discrimination in insect vision, especially when light levels are too dim to detect achromatic contrast. 4) Discovered that damselflies extend the performance range of their eyes through behavioral means, pointing their high-resolution frontal regions toward backgrounds against which visual targets will appear most conspicuous. This behavior may provide insight for the design and deployment of artificial sensory systems for target detection in low light.

## 2 Problem Statement

Many animals use sight as a primary sensory modality and rely on vision to detect, discern and localize objects of interest, whether these be potential mates, competitors, prey or predators. These tasks minimally require contrast detection and spatial resolution – that is, the ability to detect brightness or color differences between targets and their backgrounds, and the ability to locate them in space. Terrestrial habitats, however, can be exceedingly complex visual environments. Forests, for example, present a variable mosaic of vegetation, rocks, soils, and water, differentially reflecting solar illumination that itself varies strongly with time of day, season, cloud cover and forest geometry (Endler, 1990, 1993; Thery, 2001). Species that depend on visual cues for survival and reproduction are expected to have visual system adaptations that enable them to function reliably despite such detrimental photic variation (Lythgoe, 1979; Land and Nilsson, 2002; Endler, 1993). Examination of these adaptations can inspire and inform the engineering and application of artificial visual sensory systems (Horridge and Loughuet-Higgins, 1992; Nishio et al., 2004; Rajesh et al., 2005; Jeong et al., 2006).

Insects appear particularly challenged in target detection as their compound eyes have intrinsically lower light capture ability and coarser spatial resolution than the single-lens eyes of vertebrates (Horridge, 1978; Land, 1989, 1997; Land and Nilsson, 2002). The necessarily small absolute size of insect eyes and their typical apposition arrangement of simple, independent photoreceptors would seem to constrain them to application in consistently bright, diurnal environments. Yet, many insects live in dim or variously lit habitats. Are these then functionally limited, and if

so, by what means do they extend the functional capacity of their optical phenotype in order to nevertheless perform the highly demanding visual tasks required for persistence in these habitats?

Here we report results from an investigation of target detection by a territorial, aerial insect predator, the Hawaiian damselfly, *Megalagrion xanthomelas*, in a dark, riparian habitat as a model for visual sensory system design and application in a complex, visually challenging light environment. We describe the morphology of the typical apposition compound eye of diurnal insects and provide detailed measurements of the major features affecting visual performance (maximum light capture, contrast detection, and resolution) in *M. xanthomelas*. By comparing these with spectroradiometric measurements of light availability and visual backgrounds in the *M. xanthomelas* riparian habitat we identify distinct limitations imposed on visual capability by the prevailing illumination of the environment. Our research indicates two means by which these limitations are overcome. The first of these is a partitioning of the damselfly's finite visual capability across the eye so that different regions of the eye confer different advantages in the acquisition of visual information and so that maximum visual acuity in a forward "foveal" region can exceed that which would be obtained from an eye of uniform construction. The second is a behavioral strategy by which damselflies position and orient themselves within the environment so as to preferentially view backgrounds against which targets will appear most conspicuous in terms of both brightness and color contrast. To our knowledge this pattern in behavior is an entirely novel discovery in visual ecology and has not previously been quantified in any other animal. We discuss the performance gains and implications of this strategic acquisition of surveillance points and alignment of the visual field as a major component of a functionally integrated visual sensory system.

### 3 Structural design and performance of the *M. xanthomelas* compound eye

#### 3.1 Background information and methods

The typical apposition compound eye of diurnal insects is an array of adjacent sensory units or ommatidia, each with its own lens facet and radial photoreceptor structure, the rhabdom (Fig. 1). The rhabdom of each individual ommatidium collects a single light reading from the environment, and contributes a single "pixel", which is neurologically integrated with the input from other ommatidia to form the viewed image. Resolution is therefore limited by the number of lens facets and associated ommatidia that can be angled to fit to the surface curvature of the eye and view each particular region of the visual field (Land and Nilsson, 2002). Increasing the density of the ommatidial array through reduction in size of the lens facets, however, comes at the cost of contrast detection and image quality (Land, 1997). Ommatidia with smaller lenses yield lesser contrast detection due to their reduced and more variable photon capture and consequently lower signal to noise ratio (Pelli, 1990). Additionally, as ommatidia become smaller in diameter, diffraction of light at their aperture increases, resulting in blurring and degradation of optical quality. Thus, there is a general limit on overall visual capability imposed by the necessarily small absolute size

of the insect eye and fundamental tradeoff between ommatidial designs and arrangements yielding high light capture and high resolution . How is this tradeoff balanced across the approximately 1.5 mm diameter eye of an aerial insect predator in a variably illuminated environment?

To determine regional variation in *M. xanthomelas* optical design we photographed damselfly eyes mounted on a Leitz goniometer (Wetzlar, Germany) at precise angular steps under the magnification of a dissecting light microscope with coaxial illumination (Stemi DV4 spot, Zeiss). We measured lens facet diameter in reference to a stage micrometer and determined interommatidial angle using the pseudopupil technique (Horridge, 1978; Land, 1997; Rutowski and Warrant, 2002). Those ommatidia which are in line with the direction of incoming light will absorb rather than reflect that light, resulting in a black region called the pseudopupil (Fig. 3). The size of the pseudopupil when viewed parallel to the incoming light indicates the relative number of ommatidia directed at that angle (Fig. 1), and as a corollary to this, interommatidial angles can be determined as the ratio of degrees through which the eye is rotated to the number of facets over which the pseudopupil appears to move during that rotation (see Stavenga, 1979, for detailed description of the technique; Fig. 3). We mapped two transects with origins at the anterior center of the eye: a 90 degree lateral (“front” to “side” of the eye) transect and a 180 degree vertical (“top” to “bottom” of the eye) transect (Fig. 3).

From these optical morphology measurements we calculated regionalization of maximum resolution ( $\frac{1}{2 \times \text{interommatidial angle}}$ ) (Land, 1997) and light sensitivity. Light sensitivity of each ommatidia was calculated in terms of maximum photon capture ( $n$ ) (Land and Nilsson, 2002) as:

$$n = 0.62 D^2 A^2 R, \quad (1)$$

where  $D$  is the lens facet diameter in  $\mu\text{m}$ ,  $A$  is the rhabdom acceptance angle in radians, and  $R$  is the total incident radiance across wavelengths visible to the insect eye (here the mean intensity of light viewed in the habitat from 300 to 640 nm:  $0.2028 \mu\text{mol } \mu\text{m}^{-2} \text{m s}^{-1}$ ) per integration time of the rhabdom’s photoreceptors. Because the fields of view of adjacent ommatidia in the apposition compound eye abut but do not overlap, the rhabdom acceptance angle can be approximated by the interommatidial angle (Rutowski and Warrant, 2002). Integration times known from diurnal insect eyes are consistently below 0.1 s (Kelber et al., 2003; Laughlin and Weckstrom, 1993), and therefore our calculated photon capture should be interpreted as a maximum estimate.

### 3.2 Results

Our measurements of the damselfly eye indicate a pattern by which a flattening of the forward surface of the eye permits both a decrease in the interommatidial angles and a simultaneous increase in facet diameters of ommatidia in this region. Mean interommatidial angles varied from a dorsal maximum of  $5.67^\circ$  to a minimum of  $1.12^\circ$  between  $0$  and  $-5^\circ$  along the dorso-ventral transect of the eye (Fig. 4). Mean facet diameter follows the opposite pattern, increasing from dorsal,



ventral and lateral minima of 23.93, 23.43 and 22.29  $\mu\text{m}$  respectively, to a forward maximum of 34.5  $\mu\text{m}$  at 5 to 10° below the equatorial plane at the front of the eye.

These measurements indicate a single, high-resolution “fovea” (Fig. 5), directed forward and slightly downward, with maximum resolvable spatial frequency of 0.72 cycles per degree (50 cycles per radian). Therefore, the finest grating that could be resolved by the damselfly eye would be one having bands of approximately 1.2 cm when viewed from a distance of one meter. This level of visual resolution is roughly half that of the largest eyes of *Aeshna* dragonflies but still less than one hundredth that of the human eye (Land, 1981).

The high maximum visual resolution of the fovea comes at a cost in light sensitivity due to the small rhabdom acceptance angles in this region. Maximum facet diameters occur in the fovea and this provides higher light sensitivity in this region than would be obtained were facet diameters equal across the surface of the eye. Nevertheless, the ommatidia of the fovea provide the least light sensitivity, and at the mean light intensity of the damselfly’s habitat, collect less than 3% of the photons collected by the ommatidia at the top of the eye.

It has previously been recognized that the distributions of lens facet diameters and interommatidial angles of a particular compound eye reflect adaptations of that eye to habitat geometry and target characteristics (Sherk, 1978). The position of the foveal regions on the eyes relate to the specific functional requirements of predation or location and pursuit of conspecifics (Land, 1989, 1997). For example, *Anax junius*, a large dragonfly that acquires prey targets while in flight, has both conspicuous high resolution bands at the tops of the eyes for detecting overhead prey against the bright, uniform background of the sky and forward-oriented foveas used in high-speed locomotion and target tracking during pursuit (Sherk, 1978). In contrast, *Sympetrum* dragonflies that acquire flying targets from stationary positions on the ground have a single, dorsal high resolution region of low light sensitivity surrounded by an immediate periphery of moderate resolution but high sensitivity optical geometry (Labhart and Nilsson, 1995). This combination allows for reliable detection in the high sensitivity region of dark prey flying against the bright sky and for subsequent target fixation and tracking with the high resolution region during ascent, pursuit and interception (Labhart and Nilsson, 1995).

We interpret the distribution of visual capability in the eye of *M. xanthomelas* as a moderately specialized design suitable for detection of variable targets in a complex visual environment. As opposed to the dragonflies discussed above, which primarily detect targets against the simple background of the sky, *M. xanthomelas* perches and acquires targets adjacent to, or amongst, vegetation along largely shaded stream corridors and therefore contends with considerably more complex visual backgrounds. Although the most dorsal region of its eyes appears to provide substantially higher light sensitivity than any other region and could therefore serve a distinct role in initial detection of dark overhead targets against the sky, outside of this region light sensitivity and resolution vary along relatively smooth gradients across the eye. In general, discerning prey items, as well as red male and brown female conspecifics, from a variably colored and illuminated background would likely be accomplished primarily with the high resolution forward portion of the visual field. As we have found, however, this is also the region of the visual field with the least light sensitivity, and, therefore, in light limited environments the general applicability of

this design would appear to be handicapped. In the next section we discuss results indicating a compensatory behavioral strategy that maximizes the functional capacity of this design for target detection in a challenging light environment.

## 4 Site selection and orientation of visual sensors to maximize target detection in a variable environment

### 4.1 Background information and methods

Visual discrimination of targets depends on resolution, but also on detection of contrast, which is a function of both chromatic (color) and achromatic (brightness) differences between targets and backgrounds, as well as a sufficiency of light available to detect these differences (photon capture). Achromatic contrast ( $C_a$ ) between target ( $O$ ) and background ( $B$ ) radiant light intensities (in photon flux) is defined as:  $C_a = \frac{|O-B|}{O+B}$ , where a value  $C_a = 1$  indicates maximum contrast in brightness and a value of  $C_a = 0$  indicates that the target and background have the same brightness. The number of photons,  $n$ , acquired per photoreceptor needed to detect achromatic contrast,  $C$ , with 95% certainty is given by (Land and Nilsson, 2002):

$$n > \frac{1}{C^2}, \quad (2)$$

based on the statistical fluctuation of photons arriving at a photoreceptor array (described by a Poisson distribution, in which the variance is equal to the mean). Discerning a target from a background with a moderate contrast of 0.05 would therefore require photoreceptor capture of only 400 photons per integration time, whereas detection of a fine contrast of 0.01 would require 10,000 photons.

We examined whether the variably shaded habitat of damselflies potentially limits visual performance of the fovea by estimating its maximum light capture and achromatic contrast detection as oriented at perch sites. Two types of light data, irradiance and radiance, were collected with a field spectroradiometer (Ocean Optics USB 4000) for male damselflies observed perching at a typical stream-side breeding habitat (Tripler Army Medical Center, Honolulu, HI, USA – see Polhemus, 1996; Englund, 2001, for detailed description of the habitat).

*Irradiance* represents the ambient light (usually solar illumination) incident from a full hemisphere. An irradiance spectrum is reported in units of photon flux ( $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}$ ) at each wavelength of light. *Radiance* represents the light viewed by a distinct region (e.g., dorsal, frontal, lateral) of the compound eye, usually via background reflectance of habitat irradiance (i.e., the color and intensity of the visual background, Fleishman et al., 2006). Radiance is measured at a

small acceptance angle, and a radiance spectrum is reported as a radiant flux in photons per solid angle or steradian ( $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm sr}^{-1}$ ) at each wavelength of light. By comparing results for Eq. 1, the number of photons captured, to those for Eq. 2, the number of photons needed to detect a given contrast, we identified conditions under which damselfly visual discrimination of targets could be limited by brightness. Additionally we compared total radiance (background brightness) among forward and lateral views in order to determine whether damselfly perching orientations serve as a behavioral means of increasing photon capture by the fovea and thereby maximizing visual performance.

Similarly, we tested whether damselflies oriented their foveas toward backgrounds against which the specific colors of conspecifics and prey would appear most conspicuous. The radiance spectra from conspecific males and females and the typical mosquito prey (*Aedes albopictus*), as they would be viewed by the perching damselflies, was calculated as the product of the irradiance illuminating the field of view and the specific reflectance of each of these targets (Endler, 1990) measured in the laboratory at each wavelength of light (for details of reflectance measurement see Schultz et al., 2008). We used spectral segment classification (Endler, 1990) to summarize radiance spectra and estimate color contrast independent of brightness. This method provides objective measures of color (Grill and Rush, 2000), and for animals with trichromatic color vision, including some dragonflies and damselflies (Briscoe and Chittka, 2001; Schultz et al., 2008), yields an estimate of color contrast as acquired specifically by the animal’s visual photoreceptors (Endler, 1990). Radiance spectra were divided into four segments (bins) of equal wavelength ranges. By comparing the proportion of the total radiance in nonadjacent segments, each spectrum can be described according to two color opponency channels, LM (long/medium), which compares long-wavelength radiance (last segment) to shorter middle-wavelength radiance (second segment), and MS (medium/short), which compares the longer middle-wavelength radiance (third segment) with the short-wavelength radiance (first segment). Chromatic contrast between radiance spectra is the Euclidian distance between these spectra plotted as points in the two-dimensional color space defined by an LM and an MS axis.

## 4.2 Results

Light capture abilities modeled on eye morphology and perch light measurements show that the fovea and to a lesser extent the peripheral eye regions are light-limited in their ability to detect small achromatic contrasts (Fig 2; Table 1). If damselflies were to orient themselves randomly in their frontal plane at perch sites (turn randomly left or right), the fovea would view radiances permitting detection of a moderate contrast of 0.05 at less than half of these orientations, and a fine 0.01 contrast at less than 5% of these (Fig. 6). Of course, vertical orientations directing the forward visual field toward the sky would be substantially less limiting to contrast detection, but would presumably confer little benefit because conspecific and prey targets typically occur at elevations similar to those of the damselfly perches.

However, damselflies significantly improve their visual capabilities via selective orientation of their visual field. Damselflies tended to perch with the head facing at a small upward angle

( $29.2^\circ \pm 3.8^\circ$  above the horizon) slightly away from the stream corridor ( $26.0^\circ \pm 10.3^\circ$ , mean and 95% confidence interval). These orientations directed the foveas toward significantly brighter backgrounds than those of alternative lateral views in either direction (Fig. 7, Kruskal-Wallis test of medians:  $\chi^2_5 = 240.38$ ,  $P < 0.000001$ ), and yielded a two-fold increase in total radiance viewed by the forward visual field. Even the median radiance viewed by the fovea in the orientations selected by the damselflies yielded a potential to detect contrasts as fine as 0.017. If damselflies perched  $90^\circ$  left or right from their chosen orientation, contrast detection by the fovea would have been reduced by 29.2%.

Rather than providing merely a general improvement in vision through an increase in photon capture, orientation of the visual field appears to specifically increase the conspicuousness of the biologically important targets of male and female conspecifics by directing the fovea towards backgrounds against which their chromatic contrasts would be greatest. Chromatic contrast between male damselflies and backgrounds viewed by the fovea (median = 0.25) was significantly higher than that between males and backgrounds viewed by lateral regions of the eye (Kruskal-Wallis test:  $\chi^2_5 = 36.17$ ,  $P < 0.000001$ ). The perching orientations of damselflies increased forward-view chromatic contrast of males by approximately 25% over that which would be obtained had they perched  $90^\circ$  lateral from this orientation in either direction. Despite the distinct sexual dichromatism of *M. xanthomelas* (Fig. 8), the selected perching orientations also simultaneously increased the chromatic contrast of female damselflies. Chromatic contrast between the pale brown females and backgrounds viewed by the fovea (median = 0.10) was significantly higher than that between females and backgrounds viewed by lateral regions of the eye (Kruskal-Wallis test:  $\chi^2_5 = 15.61$ ,  $P < 0.0004$ ). Females are considerably more cryptic than males (Fig. 8) and the observed perching orientations provided an approximately 29% increase in their chromatic contrast over that which would be obtained from alternative lateral orientations at the same perches.

Damselflies did not perch with orientations that maximized forward view chromatic contrast between prey targets and backgrounds. In fact, forward viewed backgrounds provided the least contrast with mosquitoes (median = 0.09) and provided significantly less color contrast than backgrounds in the lateral view away from the stream (median = 0.11, Kruskal-Wallis test:  $\chi^2_5 = 8.53$ ,  $P < 0.014072$ ). Our calculations suggests that the coloration of mosquitoes would appear most conspicuous viewed more directly against the shore and vegetation bordering the stream. Therefore, the observed orientation of the fovea provided no advantage to prey detection in the forward field of view specifically through effects on chromatic contrast. For discerning a dark prey target such as a mosquito, however, the increase in viewed background brightness and achromatic contrast detection could be more important than chromatic cues.

Field tests of behavioral responses further suggest that damselflies exhibit an excellent ability to discriminate small targets based on small achromatic and chromatic cues under the variable lighting of their natural habitat. We presented perching male damselflies with 2.5 to 5 mm beads suspended from clear monofilament as artificial stimuli approximating the colors of male (red) and female (brown) conspecifics. Territorial male damselflies exhibit distinct attack and tracking responses to male and female colored stimuli respectively. Initial takeoff response and flight towards targets was initiated at distances of up to approximately 50 cm and differential responses were apparent at distances in the range of 10 cm. At either of these distances the angle

subtended on the eye would be so low that visual cues acquired from a stationary 3 mm diameter bead would be received by no more than one ommatidia even in the fovea. Clearly then, detection of biologically important targets by damselflies is sometimes a function of minimal visual stimuli.

## 5 Conclusions

These observations collectively suggest some implications for visual system limitation and design of visual sensory systems for target detection in a complex, light-limited visual environment. The visual capabilities of compound eyes may be constrained in dim habitats, even for those which are relatively large such as the damselfly. However, this can be compensated for through variation in ommatidial structure across the eye. Local regions can be enriched in resolution capability or light sensitivity, higher than those that would be obtained with uniform ommatidia. These, however, come at the expense of performance in other regions of the visual field.

An important conclusion of our research is that highly visual insects can strategically orient their visual field to achieve maximum potential target detection. This approach would be facilitated in situations in which targets possess some consistent characteristics in terms of color, overall brightness of their reflected radiances, and backgrounds possess variation in these characteristics on scales within which there is latitude to select the positions and orientations of visual sensors. Even in cases of chromatic uniformity in visual backgrounds, orientation of visual sensors towards backgrounds of greater total radiance would provide a general increase in visual capability, particularly in the detection of dark targets that would then appear conspicuous through increased achromatic contrast. For maximum reliability in an environment of variable light conditions a visual sensory system should be tuned to be sensitive to both chromatic and achromatic differences between targets and the available backgrounds.

Furthermore, damselflies possess sensitive size discrimination capabilities, as they respond maximally to objects of 3mm but less so to those which are 1mm or 5mm, this despite the fact that optical geometry would facilitate detection of larger objects (interim report, Schroeder and Butler, submitted).

As ours is the first study to report behavioral maximization of chromatic contrast as viewed by a compound eye, this strategy of exploiting environmental variation to aid in target detection remains to be fully explored. We expect that variations of this behavioral pattern will be found widespread among flying, diurnal insects that exhibit intermittent stationary perching. Most insects have relatively smaller eyes than those of damselflies and therefore would be more limited in their overall visual capability and likely more reliant on behavior to maintain an integrated functional visual sensory system. Examination of these behavioral patterns should yield general insights into strategies for positioning and orienting visual sensors for target detection in different environments much in the same way that examination of patterns in structural variation of compound eyes has led to identification of distinct morphological designs adapted to specific environments (Land, 1989, 1997). Study of insect vision should therefore provide an increasing source

of inspiration and design solutions for both the engineering and deployment of visual sensory systems, particularly as parallel advances in nanotechnology and micro-scale camera systems rapidly increase the feasibility of developing technologies directly from biological models.

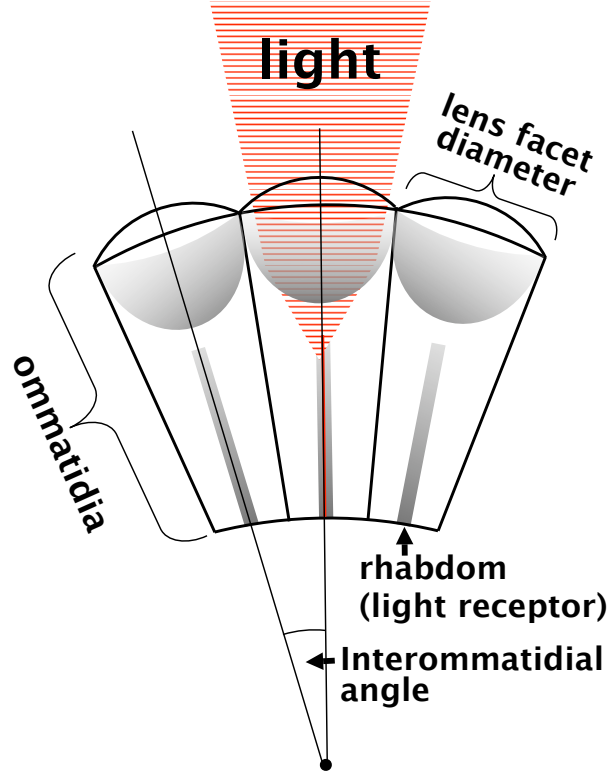


Figure 1: Basic structure of the apposition compound eye of diurnal insects. Light enters each ommatidia (individual sensory unit) through its own lens facet and is directed onto the distal tip of the light-sensing rhabdom. Decreased interommatidial angles yield higher resolution vision by increasing the number of ommatidia that view a given portion of the visual field. Higher lens facet diameters and rhabdom acceptance angles yield higher light sensitivity.



Figure 2: Light measured in directions quantifying what the damselfly sees: fordam — forward view, updam — dorsal view of damselfly, and both lateral views.  $\alpha$  indicates perch angle to the ground.

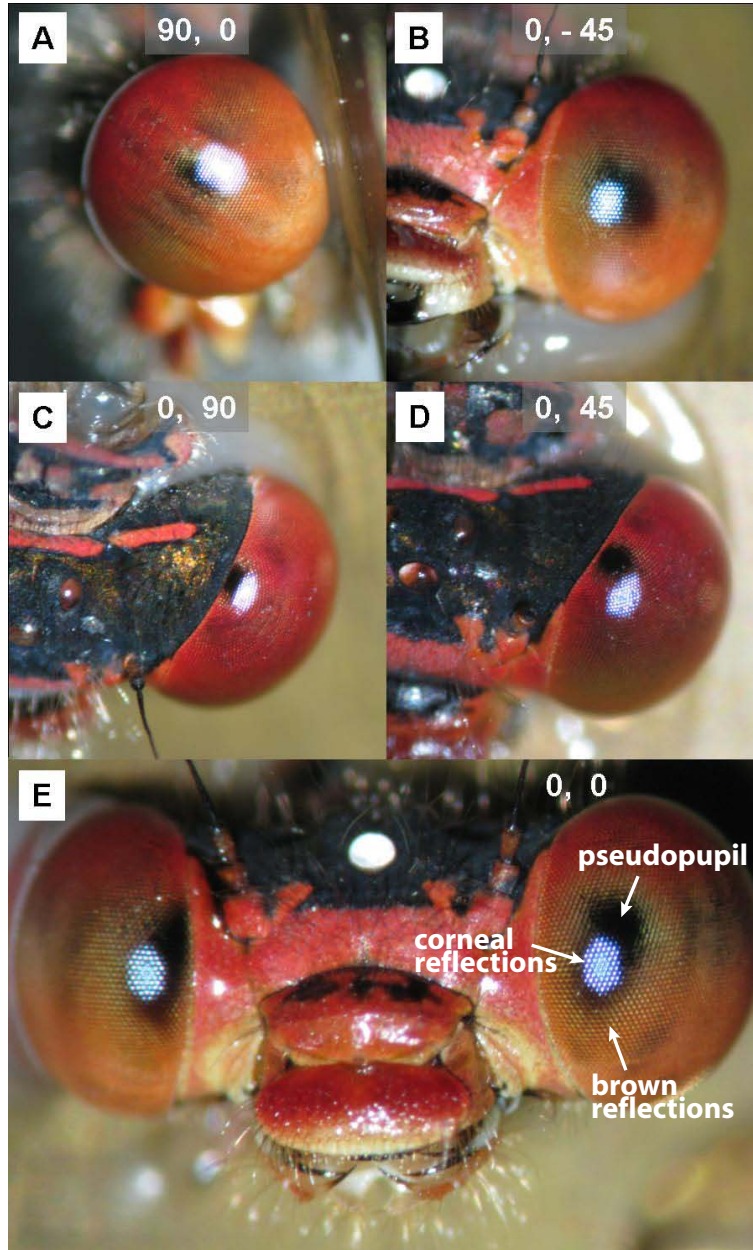


Figure 3: The size of the pseudopupil, indicating relative visual acuity, varies with viewing angle. Coordinates in each image refer to angular positions in degrees along lateral and vertical transects originating (0,0) at the anterior center of the eye. (Note that only the right eye in E is aligned to 0,0).



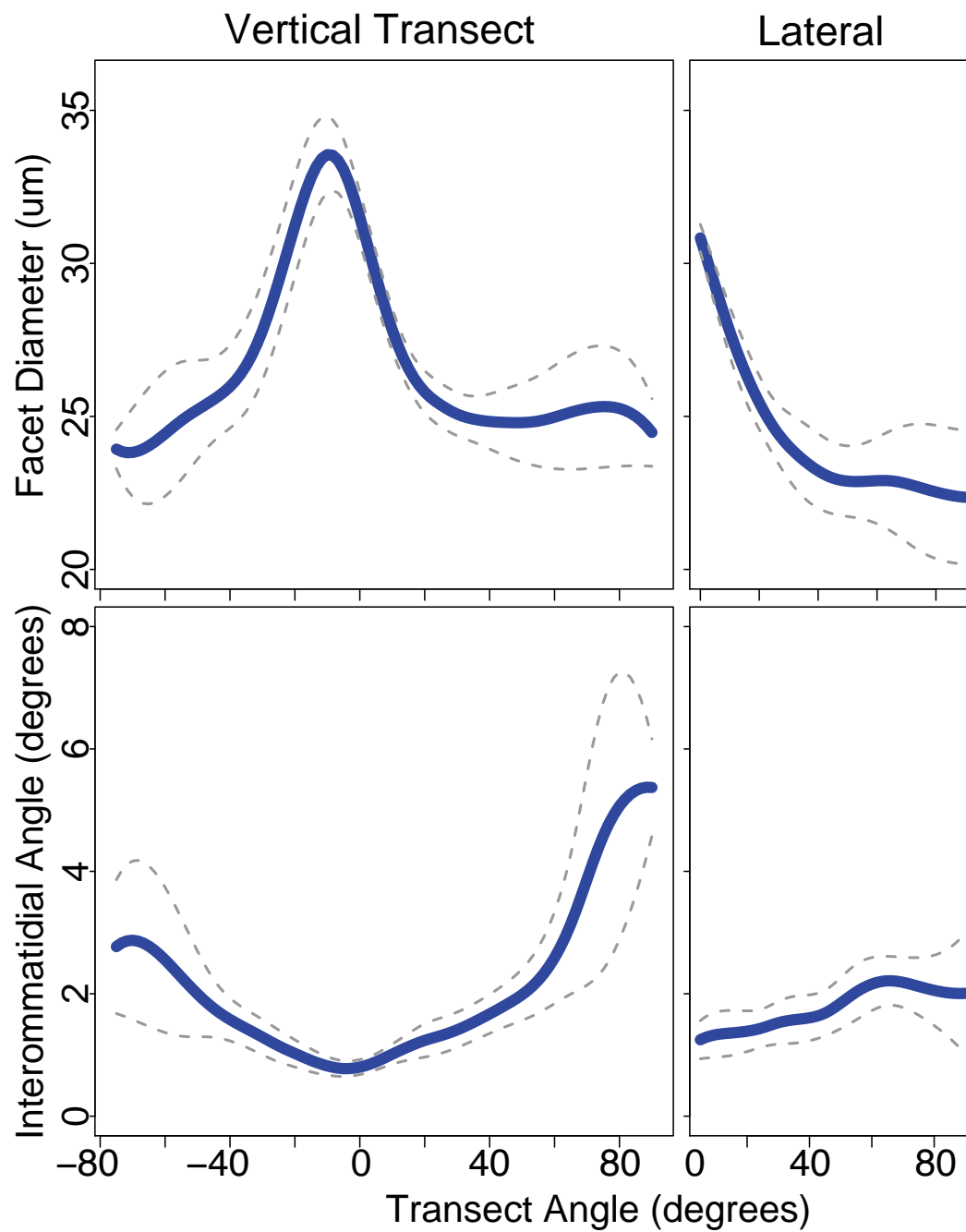


Figure 4: Regional variation in lens facet diameter and interommatidial angle along vertical and lateral transects across the eye, with 95% confidence intervals.

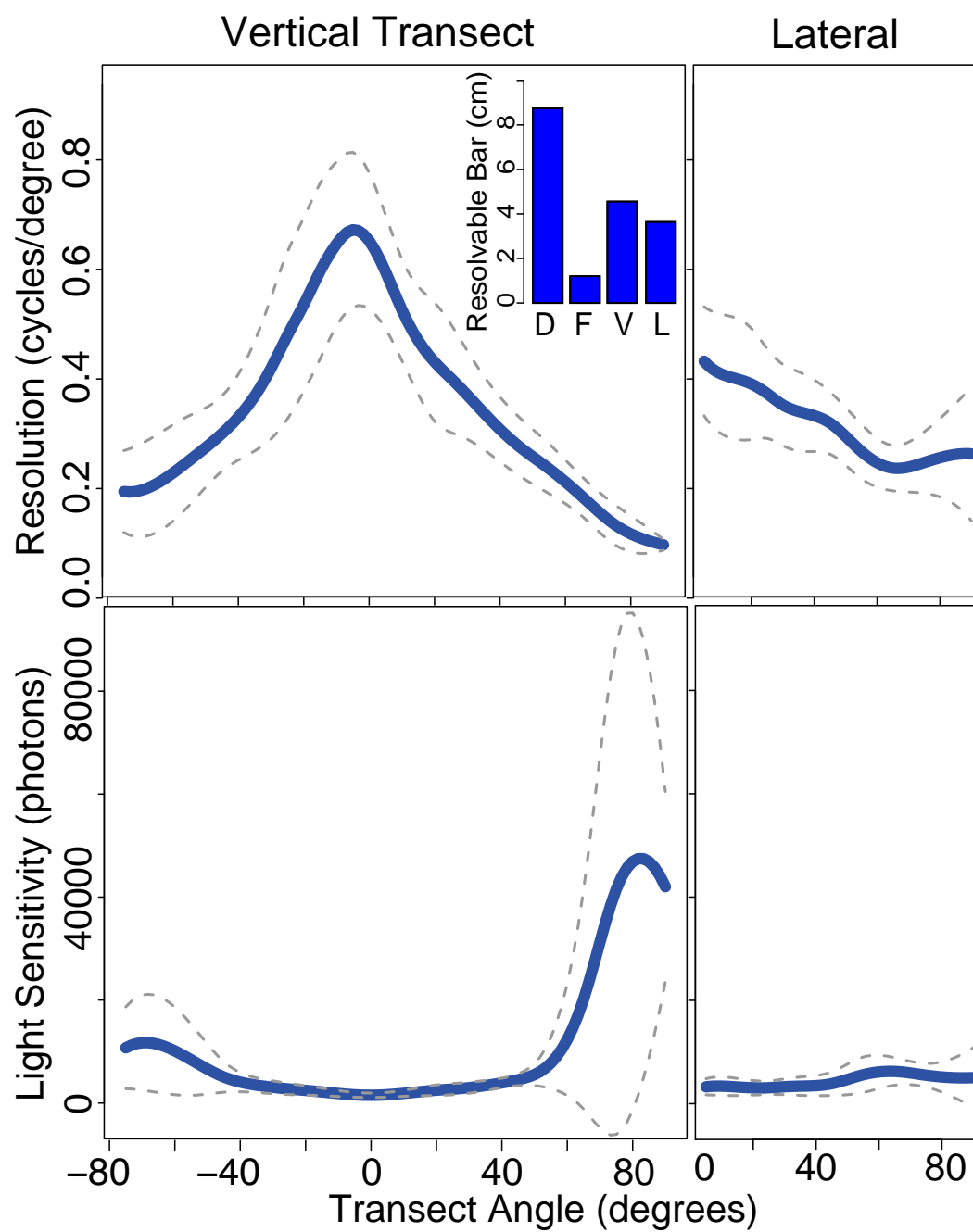


Figure 5: Resolution and sensitivity variation across the eye, calculated from lens facet diameter and interommatidial angle.

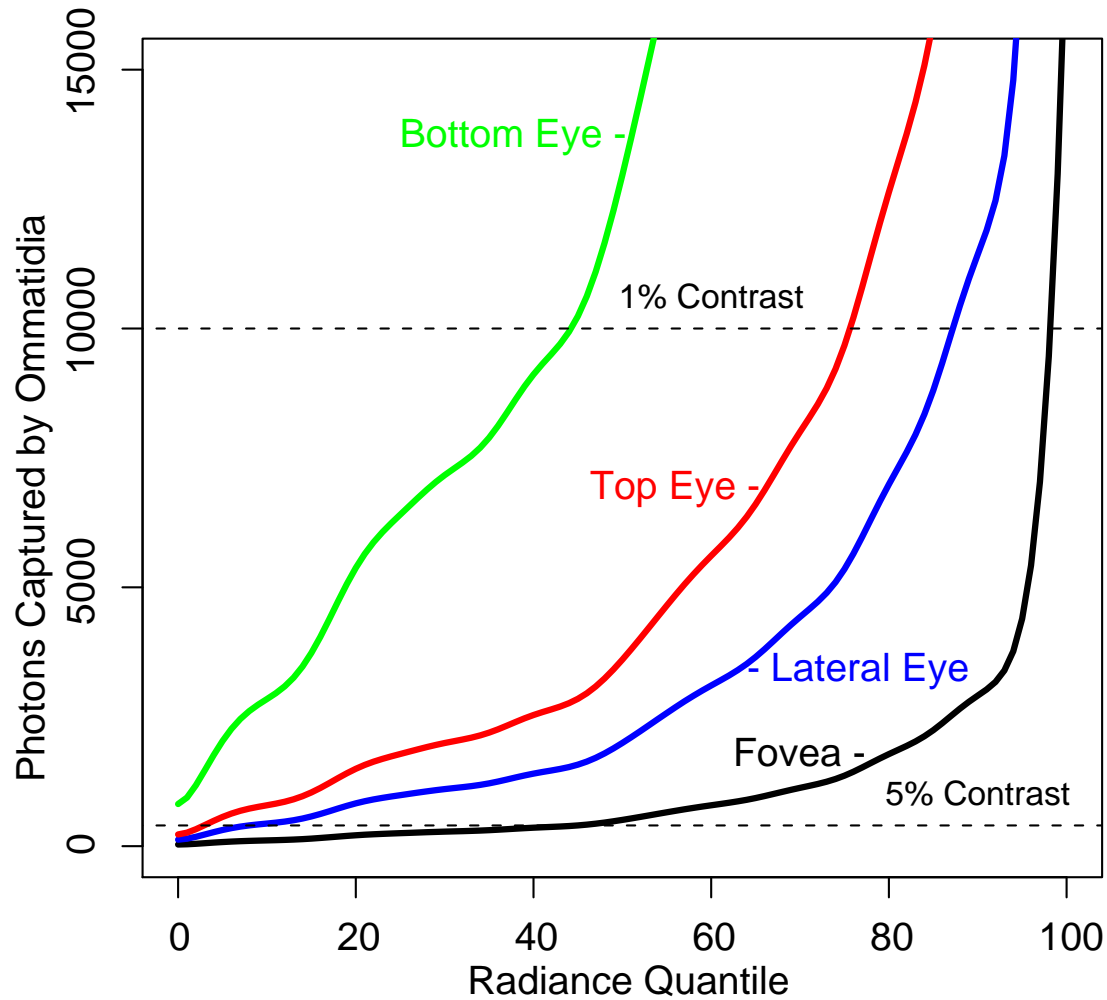


Figure 6: Photon capture by ommatidia in different eye regions calculated from lens facet diameter and rhabdom acceptance angle (estimated by interommatidial angle). Photon capture is plotted for each eye region against increasing quantiles of available habitat radiances (all forward, toward, and away from stream radiances). Photon capture in the foveal region sufficient for detection of a 1% contrast in brightness would require selection of the brightest 5% of available radiances. Lower resolution regions of the eye yield higher photon capture across all available radiances.

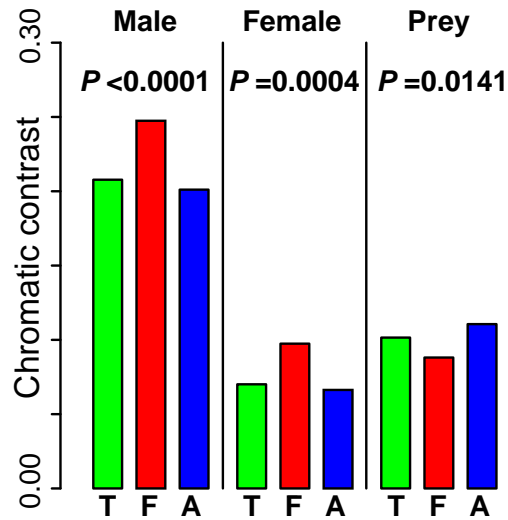
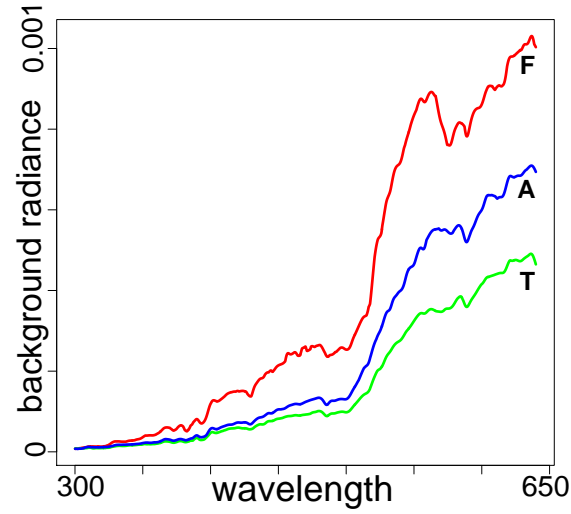


Figure 7: Median radiance spectra at perch sites from backgrounds viewed in the forward direction (F), lateral direction most toward the stream (T), and lateral direction most away from the stream and median chromatic contrast of male damselflies, female damselflies, and prey species against each of these background radiances. The selected forward view provides significantly greater chromatic contrast of conspecifics than alternative views at the same perch sites.

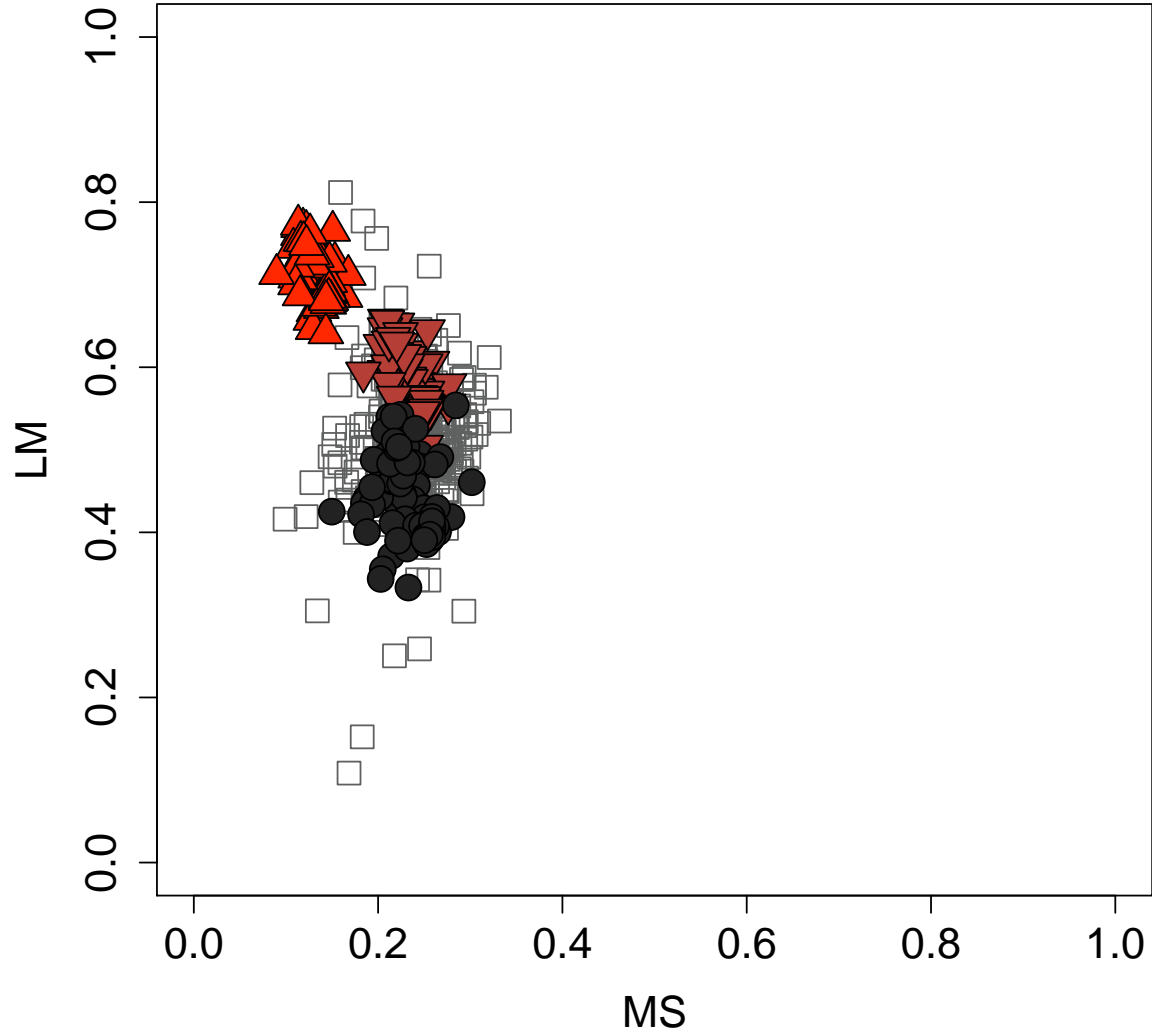


Figure 8: Radiance spectra of male (upward pointed triangles), and female (downward pointed triangles) damselflies, mosquitoes (circles), and habitat backgrounds (squares) plotted in segment classification color space. The LM axis represents the proportional contribution of long-wavelength, redder radiance to shorter middle-wavelength radiance, and the MS axis the proportional contribution of longer middle-wavelength, greener radiance to short-wavelength radiance. The distance between radiance spectra is their chromatic contrast.

Table 1: Photon capture by individual ommatidia directed at forward, lateral, and up views of the damselfly eye (see Fig 2 for orientations at perch sites). Median intensity of total radiance (300-640nm) in  $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm sr}^{-1}$ , Photons are number of photons received per integration time.

	Intensity	Photons
forward	0.132	834
toward stream	0.056	1387
away from stream	0.081	2029
up	0.536	86776

## References

- Briscoe, A. and L. Chittka. 2001. The evolution of color vision in insects. *Annual Review of Entomology*, **46**:471–510.
- Endler, J. A. 1990. On the measurement and classification of color in studies of animal color patterns. *Biological Journal of the Linnean Society*, **41**:315–352.
- Endler, J. A. 1993. The color of light in forests and its implications. *Ecological Monographs*, **63**:1–27.
- Englund, R. A. 2001. Long-term monitoring of one of the most restricted insect populations in the united states, megalagrion xanthomelas (selys-longchamps), at tripler army medical center, oahu, hawaii (zygoptera : Coenagrionidae). *Odontologica*, **30**:255–263.
- Fleishman, L. J., M. Leal, and J. Sheehan. 2006. Illumination geometry, detector position and the objective determination of animal signal colours in natural light. *Animal Behaviour*, **71**:463–474.
- Grill, C. and V. Rush. 2000. Analysing spectral data: comparison and application of two techniques. *Biological Journal of the Linnean Society*, **69**:121–138.
- Horridge, G. A. 1978. The separation of visual axes in apposition compound eyes. *Philosophical Transactions of the Royal Society of London B*, **285**:1–59.
- Horridge, G. A. and H. C. Loughuet-Higgins. 1992. What can engineers learn from insect vision? *Philosophical Transactions of the Royal Society of London B*, **337**:271–282.
- Jeong, K., J. Kim, and L. Lee. 2006. Biologically inspired artificial compound eyes. *Science*, **312**:557–561.
- Kelber, A., A. Balkenius, and E. Warrant. 2003. Colour vision in diurnal and nocturnal hawk-moths. *Integrative and Comparative Biology*, **43**:571–579. *Integrative and Comparative Biology*.
- Labhart, T. and D. E. Nilsson. 1995. The dorsal eye of the dragonfly sympetrum - specializations for prey detection against the blue sky. *Journal of Comparative Physiology A*, **176**:437–453.
- Land, M. F. 1981. *Handbook of Sensory Physiology*, volume 7, chapter Optics and vision in invertebrates, pages 472–592. Springer, Berlin.
- Land, M. F. 1989. Facets of vision, chapter Variations in the structure and design of compound eyes, pages 90–111. Springer-Verlag, Berlin.
- Land, M. F. 1997. Visual acuity in insects. *Annual Review of Entomology*, **42**:147–177.
- Land, M. F. and D. E. Nilsson. 2002. *Animal Eyes*. Oxford University Press, New York.
- Laughlin, S. and M. Weckstrom. 1993. Fast and slow photoreceptors - a comparative study of functional diversity of coding and conductances in the diptera. *Journal of Comparative Physiology A*, **172**:593–609.
- Lythgoe, J. N. 1979. *The Ecology of Vision*. Oxford University Press, New York.

- Nishio, K., H. Yonezu, A. Kariyawasam, Y. Yoshikawa, S. Sawa, and Y. Furukawa. 2004. Analog integrated circuit for motion detection against moving background based on the insect visual system. *Optical Review*, **11**:24–33.
- Pelli, D. G. 1990. Vision: Coding and Efficiency, chapter The quantum efficiency of vision, pages 3–24. Cambridge University Press, Cambridge.
- Polhemus, D. A. 1996. The orangeblack hawaiian damselfly, *megalagrion xanthomelas* (odonata: Coenagrionidae): clarifying the current range of a threatened species. *Bishop Museum Occasional Papers*, **45**:30–53.
- Rajesh, S., D. O’Carroll, and D. Abbott. 2005. Man-made velocity estimators based on insect vision. *Smart Materials & Structures*, **14**:413–424.
- Rutowski, R. L. and E. J. Warrant. 2002. Visual field structure in the empress leilia, *astrocampa leilia* (lepidoptera, nymphalidae): dimensions and regional variation in acuity. *Journal of Comparative Physiology A*, **188**:1–12.
- Schultz, T. D., C. N. Anderson, and L. B. Symes. 2008. The conspicuousness of colour cues in male pond damselflies depends on ambient light and visual system. *Animal Behaviour*, **76**:1357–1364.
- Sherk, T. E. 1978. Development of the compound eyes of dragonflies (odonata) iii. adult compound eyes. *Journal of Experimental Zoology*, **203**:61–80.
- Stavenga, D. G. 1979. *Handbook of Sensory Physiology*, chapter Pseudopupils of compound eyes, pages 357–439. Springer, New York.
- Thery, M. 2001. Forest light and its influence on habitat selection. *Plant Ecology*, **153**:251–261.